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Habitat productivity and anthropogenic development drive rangewide variation in striped skunk (*Mephitis mephitis*) abundance

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ABSTRACT

Non-charismatic species are often understudied, despite having unique ecological roles that are important to understand and value for ecosystem integrity, function, and health. Striped skunks (*Mephitis mephitis*) are one such species, as they are stigmatized and feared due to their noxious smell and potential for spreading rabies. Yet this species often co-occurs with humans, occupying a distinct but poorly understood ecological niche. To better understand this understudied species and its unique niche, we used a Bayesian N-mixture model to estimate factors driving the local abundance of striped skunks at a continent-wide scale using data from the Snapshot USA programs in 2019 and 2020. In our modelling approach, we included factors that we *a-priori* hypothesized would affect striped skunk local abundance, including habitat, agriculture, primary productivity, and anthropogenic factors. We found that skunks were most abundant in more productive and anthropogenically affected areas. The factors driving abundance (in order of effect) were primary productivity, impervious surface, cultivated land, and cultivated-wetland edge cover. While our results underscore striped skunks' role as a synanthropic species that co-occurs with humans, they are more of a synanthropic misanthrope, as their close relationship with people often causes them to suffer persecution and death. But their relationship with highly productive areas also highlights how striped skunks are habitat generalists that exploit resources in many different types of habitats. Our analysis highlights the importance of programs like Snapshot USA that collect standardized data across large geographic areas and allow broad-scale studies for evaluating the local abundance of understudied species. Using these data, we were able to provide foundational information on the relative importance of the major factors affecting the local abundance of striped skunks, with implications for the management and conservation of this unique and understudied mesocarnivore across its range.

1. Introduction

Charismatic and majestic species often act as 'flagships' for conservation (Clucas et al., 2008; Sergio et al., 2006) by drawing major interest from the public and funding from donors (Albert et al., 2018; Colléony et al., 2017). On the other end of the spectrum are

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non-charismatic species, which can be viewed as repugnant or difficult for the general public to relate to (Colléony et al., 2017). These non-charismatic species include those with distasteful eating habits like vultures, species associated with superstition like bats, or species with unpleasant smells like skunks (Davey et al., 1998). These species generally have little direct economic value or support for conservation from the public (Knight, 2008), and research surrounding them is often related to their control as nuisance species or for limiting disease (e.g., Pybus, 1988; Wood et al., 2012).

Nonetheless, while the general public may not appreciate all species, each one often has a unique ecological role that is important to understand and value for ecosystem integrity, function, and health (Bellon, 2019). For example, vultures provide critical ecosystem services by removing potentially infectious waste from the environment (Sebastián-González et al., 2021), yet their conservation is hampered by misconceptions that lead to killing by people (Lambertucci et al., 2021). Similarly, bats control insect populations and contribute to pollination and seed dispersal, but superstition and fear of disease often leads to misunderstandings and control programs rather than conservation (Lu et al., 2021). Skunks are stigmatized and feared due to their noxious smell and potential for spreading rabies, leading to lethal control programs (Clark, 1994), but are also ecologically significant due to their role as a small carnivore and host to diseases such as rabies (Gehrt, 2005; Pybus, 1988; Tardy et al., 2014). Understanding species' rangewide distribution and abundance, including which factors drive these patterns, is critical to inform conservation and management (Fryxell et al., 2014; Guisan and Thuiller, 2005). Further, broad-scale studies are especially needed for understudied species because the results of local studies often fail to generalize across geographic distributions (Allen et al., 2022; Moll et al., 2016).

Striped skunks are a small, synanthropic carnivore (i.e., an undomesticated animal that lives close to and benefits from humans) that are best known for their noxious smell and coloration (Jackson et al., 2021; Larivière and Messier, 1996), and inhabit a unique ecological niche in North America. To deter predatory attacks, skunks have developed aposematic (black and white) coloring as a warning (Hunter, 2009; Larivière and Messier, 1996), and anal scent gland secretions that can be accurately sprayed as a defensive or offensive weapon (Allen et al., 2016; Hunter, 2009). In interactions with humans, the noxious smell can be unpleasant when skunks den under houses and causes fear of spraying pets and children. As a small carnivore, striped skunks are prone to predation from large carnivores such as pumas (*Puma concolor*), coyotes (*Canis latrans*), and great horned owls (*Bubo virginianus*) (Hunter and Caro, 2008), but their adaptations generally protect them from smaller carnivores that are more similar in size such as gray foxes (*Urocyon cinereoargenteus*) (Allen et al., 2016; Gehrt, 2005). Striped skunk range expanded due to forest clearing following European colonization of North America (Rosatte, 1987). Despite their extensive range, striped skunks are understudied, with little understanding of their ecology or factors that affect their abundance beyond basic natural history (Bateman and Fleming, 2012; Rosatte, 1987). This lack of information is surprising given the unique niche skunks inhabit and that skunks are the target of large expenditures for pest management and rabies control across North America (Fehlner-Gardiner, 2018; Pybus, 1988).

The modest body of research on striped skunks suggest they are a synanthropic omnivore, that often co-occurs with humans and has several habitat preferences, but variation in study findings across their range, especially with respect to habitat, is substantial (Schneider et al., 2019). For example, skunks have been shown to be positively associated with greater housing densities (Nickel et al., 2020; Suraci et al., 2021), and both negatively and positively associated with greater proportions of impervious cover (Moll et al., 2020a; Ordeñana et al., 2010). Similarly, striped skunks can be negatively (Nickel et al., 2020) or positively (Suraci et al., 2021) associated with higher human population densities. Roads represent a major potential limiting factor for skunk populations due to vehicular strikes, which are a leading cause of striped skunk mortality (Bateman and Fleming, 2012; Gehrt, 2005). Striped skunk diet is broad and seasonally variable, shifting from predominately animal and insect matter in spring and summer to a more omnivorous diet in fall that contains substantial amounts of fruits and plant material (Rosatte, 1987). Striped skunks have been found to select for wetland and edge habitats (Bixler and Gittleman, 2000; Larivière and Messier, 2000), and select for (Bixler and Gittleman, 2000) and against (Larivière and Messier, 2000) forest habitats. Selection for agricultural areas is mixed, with a general avoidance of crops, but selection for agricultural corridors and undisturbed ground (Tardy et al., 2014).

To understand the ecological niche of striped skunks, it is necessary to understand the factors that drive their local abundance, including habitat and anthropogenic features. We used a Bayesian N-mixture model to estimate factors driving the local abundance of striped skunks at a continent-wide scale. Our objective was to determine the factors that drive skunk abundance at sites across the contiguous USA. In our modelling approach, we included factors that we *a-priori* hypothesized would affect the local abundance of striped skunks. Among habitats, we expected edge habitat and wetlands to have a positive effect on striped skunk abundance (Hwang et al., 2007; Larivière and Messier, 1998) and forest habitats to have negative effects (Larivière and Messier, 2000). We also expected primary productivity and housing density to have positive effects on striped skunk abundance (Nickel et al., 2020; Suraci et al., 2021; Willig et al., 2003). Previous research has shown mixed effects on striped skunks for multiple variables, including cultivated land, population density, and impervious cover, and we also tested these in order to clarify their effects across large spatial scales. Our goal is for these analyses to provide foundational information on the relative importance of the major factors affecting the local abundance of striped skunks, with implications for the management and conservation of this unique and understudied mesocarnivore across their range.

2. Materials and methods

2.1. Study area

We used camera trap data collected during the nationwide Snapshot USA 2019 and 2020 campaigns (Cove et al., 2021; Kays et al., 2022a) to assess the local abundance of striped skunks. We did not include camera trap data from Alaska or Hawaii because striped skunks do not occur in these states, and instead focused our analyses on the contiguous USA. Data in the remaining subset were

collected from two coordinated surveys of 2955 individual camera trap sites from 207 camera trap arrays between August 8, 2019 and November 24, 2019 and between July 14, 2020 and December 3, 2020. Data was primarily collected in September and October, with 95.6% of skunk detections (2019 = 98.1%, 2020 = 93.4%) and 95.8% of trap nights (2019 = 90.4%, 2020 = 97.5%) in September and October. Camera trap arrays were established as part of the Snapshot USA program or were subsets of long-term camera trap studies, and sites and arrays were determined by Snapshot USA participants. Camera arrays ranged from 25.17° to 48.41° latitude and from –124.21° to –68.66° longitude. Camera trap arrays surveyed a diversity of mammal and ecological communities as well as all major climatic, land cover and landscape types across the contiguous USA.

2.2. Data collection

Camera trap arrays were established with the goal of obtaining a minimum of 400 trap nights per array. Camera trap sites were active for an average of 34.92 survey days (SD = 18.90, max = 142, min = 1), totaling 103,139 survey days. Spacing between camera trap sites typically ranged between 200 and 5000 m within arrays. Camera trap models used in the study were reasonably similar with comparable trigger speeds and high-resolution photos (Cove et al., 2021; Kays et al., 2022a), and were generally deployed ~30–50 cm off the ground. Camera traps were generally programmed to take bursts of 3 photos at each detection without a quiet period between triggers. We considered species detections at the same camera trap site to be independent when more than one minute apart, based on previous research that quantitatively examined independence in camera trap events and showed that events with a one minute interval lacked correlation for striped skunks and other species (Kays and Parsons, 2014). Each photo was reviewed by two experts, and striped skunks are easily differentiated from other species (Kays et al., 2022b). Further specifics on camera trap arrays and associated details can be reviewed in the publication for each year of data (Cove et al., 2021; Kays et al., 2022a), but we accounted for variation in sampling among arrays by explicitly including survey effort (trap nights) and year (2019 or 2020) as factors in our modelling as explained below.

We developed a suite of covariates at the scale of the camera trap site (100 m buffer around each camera trap site). We chose this buffer because previous research suggests that it is at this spatial scale that striped skunks respond most strongly to habitat variation during summer and fall (Moll et al., 2020a; Nichols et al., 2008). We extracted covariates using QGIS v3.12 (QGIS Development Team), and the packages landscapemetrics, sf, and raster in RStudio (Hesselbarth et al., 2019; Hijmans and van Etten, 2016; Pebesma, 2018; R Core Team, 2021). A complete description of these covariates and their justifications are provided in Table 1, and the full dataset is available in Supplementary Material 1.

2.3. Statistical analyses

We used program R version 4.0.2 (R Core Team 2020) for our statistical analysis. We prepared skunk count histories, where cells represented the total number of individual skunks detected during each sampling occasion, using the 'camtrapR' package version 2.0.3 (Niedballa et al., 2016) for N-mixture modelling. Each replicate sampling occasion consisted of seven consecutive camera trap days. We chose seven-day sampling occasions to both reduce bias in count estimates (Kendall and White, 2009) and increase skunk detection

Table 1

The description and hypothesis/reason for all covariates considered in our initial model. Each covariate was created using a 100 m buffer around each camera trap site. We created covariates using QGIS v3.12 (QGIS Development Team), and RStudio (R Core Team, 2021). Data for covariates are provided in Supplementary Material 1.

Covariates	Description	Hypothesis/Reason
Cultivated Land Cover	Proportion of cultivated land	Striped skunks select for (Tardy et al., 2014) or against (Larivière and Messier, 2000) agricultural habitats
Cultivated-Wetland Edge Cover	Edge density between cultivated and wetland land	Striped skunks often move and den along edges of wetlands and cultivated land (Hwang et al., 2007; Larivière and Messier, 1998)
Forest Cover	Proportion of deciduous, conifer, or mixed forest cover	Striped skunks select against forest habitats (Larivière and Messier, 2000)
Forest-Urban Edge Cover	Edge density between forest and urban land	Striped skunks often use urban areas including along edges of forests
Gross Primary Productivity	Normalized difference vegetation index (NDVI)	Mammals are usually more abundant in areas with greater productivity due to more abundant food resources (Willig et al., 2003)
Housing Density	Houses per km ²	Striped skunks are positively affected by greater housing densities (Nickel et al., 2020; Suraci et al., 2021)
Impervious Cover	Proportion of land cover that is impervious surface	Striped skunks are positively (Moll et al., 2020a) or negatively (Ordeñana et al., 2010) affected by greater proportions of impervious cover
Latitude	The latitude of a given site	Used as a control for potential spatial autocorrelation from unmodeled factors (Rota et al., 2016)
Longitude	The longitude of a given site	Used as a control for potential spatial autocorrelation from unmodeled factors (Rota et al., 2016)
Population Density	People per km ²	Striped skunks can be negatively (Nickel et al., 2020) or positively (Suraci et al., 2021) affected by greater numbers of people (Nickel et al., 2020; Suraci et al., 2021)
Road Density	Roads per km ²	Vehicular strikes are a leading cause of striped skunk mortality and roads will have a negative effect on them (Gehrt, 2005)
Trap Nights	The number of nights each camera trap site was active	Animals are more likely to be detected when monitored over longer time periods
Wetland Cover	Proportion wetland cover	Striped skunks select for wetland habitat (Larivière and Messier, 2000; Phillips et al., 2003)

probabilities to help improve model convergence. In this manner, estimated counts per site reflect an index of relative abundance across sites (hereafter referred to as “local abundance”) and can be interpreted as the estimated number of skunk detections per week.

We modelled striped skunk local abundance across the contiguous United States by applying a modified version of a co-abundance N-mixture model (Amir et al., In Review) into a single-species, two-season Bayesian N-mixture model. We chose this model over other N-mixture approaches (Blasco-Moreno et al., 2019; Kéry and Royle, 2015; Royle, 2004) because it allowed us to control for both zero-inflation in striped skunk detection/non-detection at a given array and for overdispersion in estimated counts per site within arrays. Additionally, we chose N-mixture modelling instead of other recently-developed methods for abundance estimation from camera trap surveys such as Time to Event models and Space to Event models (Moeller et al., 2018) because the Snapshot USA protocol does not adequately capture the data required for these methods (e.g., skunk movement rates). Specifically, we modelled local abundance, N_i , as:

$$N_i \sim \text{Poisson}(\lambda_i * Z_j)$$

where λ_i denotes the expected number of skunks detected per week at site i , and Z_j represents a zero-inflation parameter that accounts for the detection/non-detection status of striped skunks at array j . Z_j was 1 if striped skunks were detected at a given array, and 0 if not. By fixing local abundance to 0 when skunks were not detected instead of estimating non-zero counts at these sites, we were able to both minimize type 1 error and improve model convergence (Amir et al., In Review; Martin et al., 2005). We modelled the effects of anthropogenic and environmental factors on striped skunk local abundance as:

$$\log(\lambda_i) = \alpha_{\text{year}} + \alpha_{\text{covs}} * X_i + \alpha_{\text{lat}} * \text{Lat}_i + \alpha_{\text{long}} * \text{Long}_i$$

where α_{year} is a year-specific intercept, α_{covs} is a vector of covariate effects for the site-specific covariates included in the final model and explained below, X_i is the vector of site-specific covariates included in our final model (Table 1), α_{lat} is the covariate effect of site-specific latitude (Lat_i), and α_{long} is the covariate effect of site-specific longitude (Long_i). We assessed “significance” of model parameter estimates by assessing the posterior mean and whether the 95% Bayesian Credible Interval (CI) overlapped zero. If zero was not included in parameter CI, we interpreted this as a “statistically significant” effect. Since multiple covariates were correlated with other predictors (Pearson’s $|r| > 0.70$), we crafted our final model by first running univariate models using each covariate as a predictor of local abundance while holding our detection model constant (the parameters of which are explained below). We elected to retain all predictors that produced a “significant” univariate signal (as explained above) in the final model. If collinear predictors both produced “significant” signals, we excluded the one whose coefficient was smaller in magnitude (Allen et al., 2022). For example, both human population density and housing density produced “significant” positive signals, but each were correlated with percent impervious surface cover, which produced a larger signal, and hence we excluded both human population density and housing density from the final model. We also included both latitude and longitude in our final model to account for spatial clustering within the dataset (Cove et al., 2021; Kays et al., 2022a). Before analysis, we standardized all covariates to have a mean = 0 and a standard deviation = 1, which improved numerical optimization and allowed for direct comparison of effect sizes across predictors (Allen et al., 2022; Schielzeth, 2010).

We accounted for imperfectly observed local abundance during sampling occasions by assuming that the detection of striped skunk at site i during sampling occasion k , $n_{i,k}$, follows a binomial distribution:

$$n_{i,k} \sim \text{Binomial}(N_i, p_{i,k})$$

where $p_{i,k}$ represents striped skunk detection probability at site i during sampling occasion k . We then modelled the effects of covariates on skunk detection probability as:

$$\text{logit}(p_{i,k}) = \beta_{\text{year}} + \beta_{\text{prod}} * \text{Productivity}_i + \beta_{\text{effort}} * \text{Effort}_i + \varepsilon_{i,k}$$

where β_{year} represents a year-specific intercept term, β_{prod} represents the modelled effect of site-specific Normalized Difference Vegetation Index (NDVI; Productivity_i), β_{effort} represents the modelled effect of site-specific survey effort (calculated as the total number of days a site was active; Effort_i), and $\varepsilon_{i,k}$ represents an occasion and site-specific overdispersion random effect parameter that follows a normal distribution:

$$\varepsilon_{i,k} \sim \text{Normal}(0, \sigma)$$

where σ represents the standard deviation of $\varepsilon_{i,k}$. We included both NDVI and effort as covariates in the detection model because both vegetation density and the number of survey days could affect the detection of skunks at a given site.

We estimated all model parameters within a Bayesian framework using Markov Chain Monte Carlo (MCMC) methods in program R using the package ‘jagsUI’ (Kellner and Meredith, 2019). We ran three chains in parallel, each consisting of 40,000 iterations. We discarded the first 20,000 iterations as burn-in following an adaption phase of 20,000 iterations. We did not thin chains (Link and Eaton, 2012), resulting in 60,000 samples retained to craft each parameter’s posterior distribution. We used a normal prior distribution with a mean = 0 and variance = 1000 for all parameters except σ , which we used a Uniform (0, 10) distribution. We assessed model convergence by calculating the Gelman-Rubin statistic, where values < 1.1 indicate convergence across chains (Gelman, 2004), and by inspecting parameter traceplots. Finally, we assessed model fit using a Bayesian p -value and a \hat{C} score calculated from both simulated and observed data (Allen et al., 2022; Suraci et al., 2021), where Bayesian p -values between 0.25 and 0.75 indicate a good fit and a \hat{C} score less than 1.1 suggests that minimal overdispersion remains unaccounted for (Conn et al., 2018; Gelman et al., 1996; Mazerolle,

2017). Both values were calculated using chi-squared discrepancy statistics (Allen et al., 2022; Kéry and Schaub, 2011; Suraci et al., 2021). We compared covariates with significant relationships based on their β coefficient values and Bayesian Credible Intervals (CIs).

3. Results

The dataset included 751 total detections (2019 = 350, 2020 = 401) of striped skunks across the contiguous U.S.A. Striped skunks were detected at 86 of 207 camera trap arrays (41.5%), and at 230 of 2954 camera trap sites (Fig. 1), resulting in a naïve site use probability estimate of 7.8% at the camera trap level.

The N-mixture model had an excellent fit to the data with a Bayesian p -value of 0.53 with a small amount of overdispersion unaccounted for ($\hat{C} = 1.13$). Model convergence was excellent for all monitored parameters (Gelman-Rubin statistic < 1.1) except the detection probability estimate for 2020, which was 1.11 (Table 2). Our model for striped skunk local abundance (i.e., expected weekly count) ranged from 0 to 18.78, with a mean of 0.90.

Skunk detection probability did not change across years ($\beta_{\text{year-2019}} = -5.4$, 95% CI = -6.1 to -4.62 ; $\beta_{\text{year-2020}} = -5.05$, CI = -5.81 to -4.31 ; Table 2). Skunk detection probability was negatively associated with NDVI ($\beta_{\text{productivity}} = -1.81$, CI = -2.26 to -1.35), and survey effort did not have a significant effect on skunk detection probability ($\beta_{\text{effort}} = -0.22$, CI = -0.45 to 0.01 ; Table 2).

Skunk local abundance did not change significantly across years either ($\alpha_{\text{year-2019}} = 0.48$, CI = 0.05 – 0.89 ; $\alpha_{\text{year-2020}} = 0.25$, CI = -0.15 to 0.67). Skunk local abundance increased in the southwest, with negative associations with both latitude and longitude ($\alpha_{\text{lat}} = -0.41$, CI = -0.54 to -0.29 ; $\alpha_{\text{long}} = -0.38$, CI = -0.52 to -0.25 ; Fig. 1).

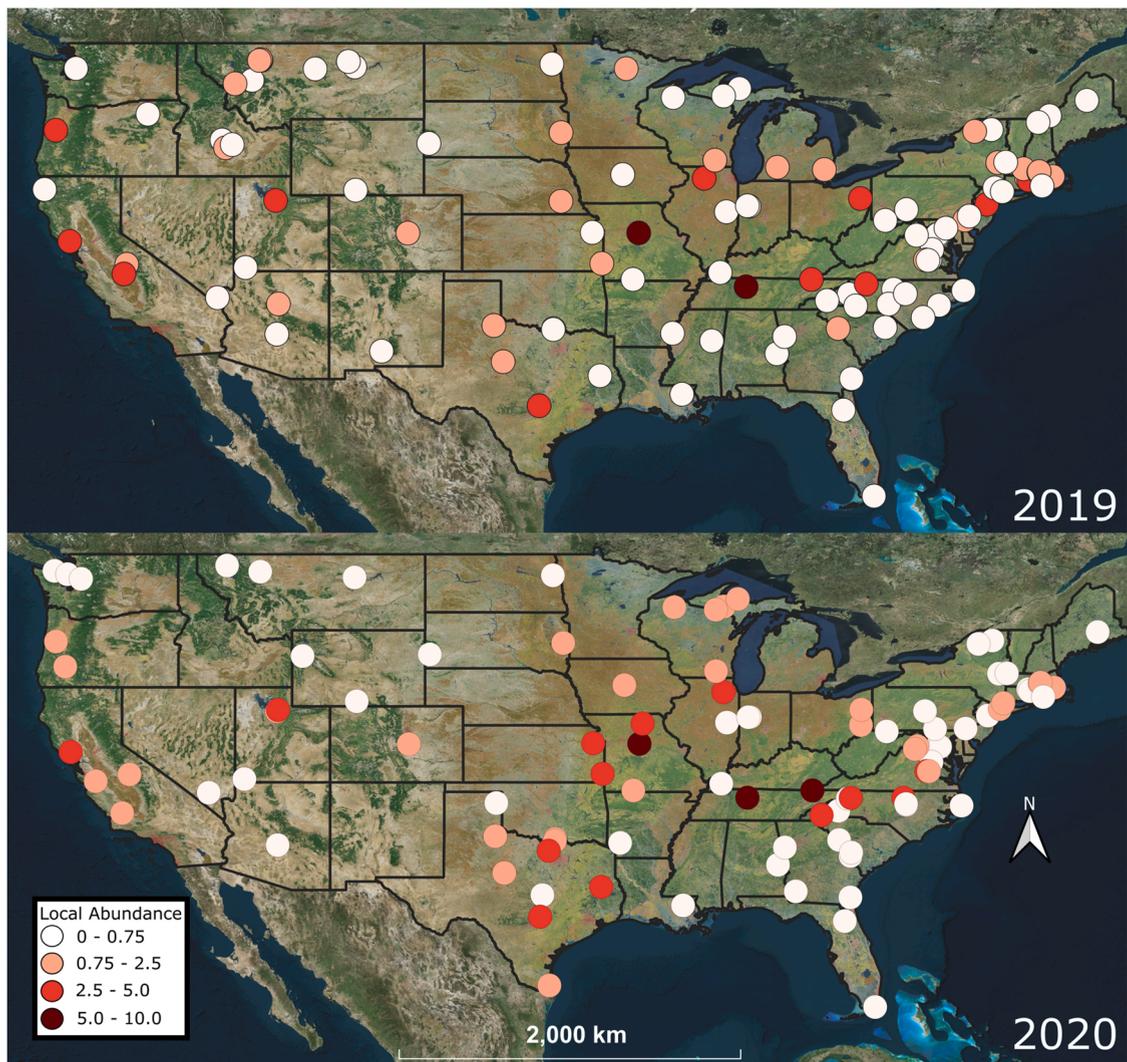


Fig. 1. Model-predicted local abundance of striped skunk across the contiguous U.S.A. Models were fit to data collected from 2954 sites during fall 2019 and 2020. Each circle represents the mean local abundance for a camera trap array (see main text).

Table 2

The results for each detection and count covariate that we included in the final model (i.e., each variable that was significant when run as a univariate model). We provide the mean and 95% credible intervals (CI). We considered covariates that had their CI overlap with zero to be non-significant and marked these in italic font.

Parameter	Mean	95% CI
Detection		
NDVI	-1.81	-2.26 – - 1.35
<i>Trap Nights</i>	<i>-0.22</i>	<i>-0.45 – 0.01</i>
Count		
Latitude	-0.41	-0.54 – - 0.29
Longitude	-0.38	-0.52 – - 0.25
Impervious Surface Cover	0.34	0.16 – 0.52
NDVI	0.88	0.60 – 1.16
Cultivated Land Cover	0.16	0.07 – 0.24
Wetland Cover	-0.21	-0.42 – - 0.01
Cultivated-Wetland Edge Cover	0.11	0.04 – 0.20

Local abundance for striped skunks was positively associated, ordered from strongest to weakest effect size, with primary productivity (e.g., NDVI; $\alpha_{ndvi} = 0.88$, CI = 0.60 – 1.16; Table 2), impervious surface cover ($\alpha_{imp} = 0.34$, CI = 0.16 – 0.52), cultivated land cover ($\alpha_{cult} = 0.16$, CI = 0.07 – 0.24), and cultivated-wetland edge cover ($\alpha_{cult-wet} = 0.11$, CI = 0.04 – 0.20; Fig. 2). Finally, local abundance was negatively associated with wetland land cover ($\alpha_{wet} = -0.21$, CI = -0.42 to -0.01).

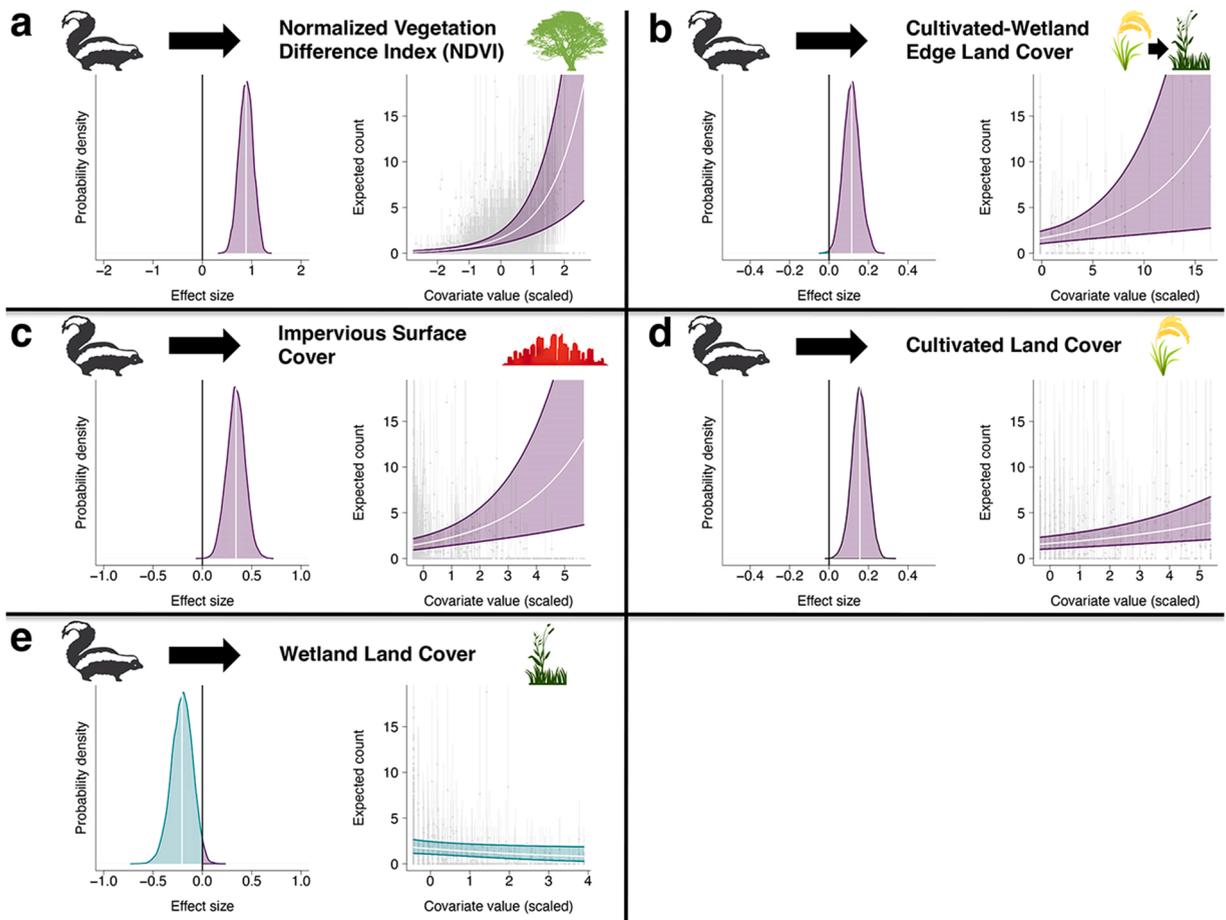


Fig. 2. Skunk local abundance in response to a) NDVI, b) cultivated-wetland edge land cover, c) impervious surface cover, d) cultivated land cover, and e) wetland land cover. Curves on the left side of each plot represent the posterior distributions of the accompanying covariate effect parameter. Plots on the right represent the association of each covariate with estimated skunk local abundance. Dots and associated error bars represent site-specific local abundance estimates with associated 95% Bayesian Credible Intervals (CI). The white line represents the mean estimated effect, with shaded regions representing the effect 95% CI. Light blue color represents negative effects, while purple color represents positive effects.

4. Discussion

We modelled the direction-corrected relative abundance of striped skunks, a widespread but understudied small carnivore, using large, standardized camera trap datasets at a continental-scale across the contiguous USA and found that skunks were most abundant in highly productive and anthropogenically affected areas. The main factors driving abundance were (in order of effect) primary productivity, impervious surface, cultivated land, and cultivated-wetland edge cover, all of which can be related to highly productive areas or areas with greater anthropogenic effects in the form of impervious surface and agriculture. The aposematic coloring and noxious odors that skunks have developed protect them from predation from most carnivores in North America (Hunter and Caro, 2008), especially east of the Rockies. This general lack of fear from predation may allow skunks to focus their habitat selection primarily on food acquisition, and as such, the selection for a diverse array of habitat features may be due to their broad diet (Larivière and Messier, 2000; Rosatte, 1987). This is likely most reflected in the result of primary productivity having the strongest effect on skunk local abundance, with primary productivity likely being a good proxy for their diverse omnivorous diet.

Striped skunks are often thought of as synanthropic species because they often co-occur with humans, but are likely more of a “synanthropic misanthrope”; a term that has been used to describe other urban-associated species that also suffer persecution like coyotes (*Canis latrans*; Gehrt et al., 2011). We found positive relationships with impervious cover, housing density, and population density, supporting findings of previous research (Moll et al., 2020a; Nickel et al., 2020), but also contradicting results found from other investigations (e.g., negative relationship with surface cover; Ordeñana et al., 2010). However, habitat selection for or against anthropogenic development can be confounded by the multitude of metrics used to classify urbanization (Nickel et al., 2020) and the scale at which these variables are calculated (Moll et al., 2020a). This can create difficulties when making comparisons across studies, and may explain the amount of variation in studies of the effects of anthropogenic factors on skunks. Overall, our results underscore how “urbanization” is not one monolithic concept and that species likely have variable responses to specific urban features (McIntyre et al., 2008; Nickel et al., 2020; Suraci et al., 2021). Furthermore, while the scale of a variable considered is important, small spatial scales (i.e., around camera trap sites) like the scale we analyzed tend to be the scale at which skunks most strongly respond to habitat and urbanization metrics (Moll et al., 2020a; Nichols et al., 2008). The relationship of skunks with anthropogenic development could be due to the tendency of skunks to seek out human subsidies and to den in or near built structures in both rural and urban areas (e.g., under farm barns or in residential yards, respectively), or selection for anthropogenic metrics is related to other metrics, such as primary productivity or other resources (e.g., denning sites) being available in areas associated with higher impervious surface. But this relationship of skunks with anthropogenic development is not always to the long-term benefit of skunks, as the unique scent of skunks is easily recognizable and frequently causes fear in humans. As a result, direct human persecution (being lethally removed when found near houses) is a leading cause of mortality in some areas (Hansen et al., 2004), as are vehicular strikes on roads (Bateman and Fleming, 2012; Gehrt, 2005). Thus, while striped skunks are a synanthropic species often found near anthropogenic habitats, this habit also leads them to suffer as a result.

Our results are generally in agreement with our hypotheses (Table 1) and past research, although previous studies have reported variation and conflicting results regarding habitat selection (Schneider et al., 2019). Habitat type and availability has been found to not affect skunk home range size (Bixler and Gittleman, 2000), suggesting that skunks are habitat generalists that exploit resources in many different types of habitats and this may explain much of the variation among studies. The local abundance of striped skunks had a positive relationship with cultivated land, as well as cultivated-wetland edge. While cultivated land can be both highly productive and a source of food, skunks have been found to avoid agricultural fields during the day (Tardy et al., 2014), suggesting that their habitat use does sometimes change based on perceived risk. While selection for cultivated land has been found to be mixed, striped skunks have been found to sometimes select strongly for agricultural corridors (such as hedgerows along fields; Tardy et al., 2014). Striped skunks have also been found to select for edge habitats (Bixler and Gittleman, 2000; Larivière and Messier, 2000; Phillips et al., 2003), which tend to be productive areas with abundant food (Bixler and Gittleman, 2000; Phillips et al., 2003) and other resources (such as dens; Bailey, 1971; Bixler and Gittleman, 2000; Storm, 1972). Striped skunk dens are often found along edges of wetlands and cultivated land (Hwang et al., 2007; Larivière and Messier, 1998), possibly explaining positive relationship between abundance and edge habitat in our model (Fig. 2b). We also found no relationship between skunk local abundance and forest habitats, which supports the conclusions of previous research (Larivière and Messier, 2000).

Our results indicated that the local abundance of striped skunks did not change annually, but there was variation regionally highlighting the value of continent-wide monitoring programs (Fig. 1). Detection of striped skunks was also similar across both years, and detection was unaffected by the number of trap nights at a camera site. The negative relationship between detection and NDVI is likely due to viewshed obstruction by understory plants in productive areas. We included this covariate in the detection model to help reduce bias in our abundance estimates (Moll et al., 2020b). Since most data for Snapshot USA was collected in September and October, this likely minimized seasonal variation in detection and abundance. Across the two years of the study, local abundance of skunks was higher in the southwest and decreased in the northeast. This pattern, and our overall estimates of local abundance, may have been affected by our metric of local abundance, which could be a reflection of multiple individual skunks or multiple detections of the same individual skunk across repeat sampling occasions. Finally, it is important to note that the Snapshot USA dataset, although covering all of the contiguous U.S.'s major ecoregions and being generally representative of habitat variability across the country, is gathered near urban areas, and there are large swaths of land with no sampling effort. Therefore, although we believe these results illustrate accurate striped skunk local abundance trends in response to both environmental and anthropogenic factors across the majority of its range, we acknowledge that it does not fully encompass all habitats where skunks are present and that localized differences in habitat preference may be present in areas with less sampling effort within the Snapshot USA dataset.

Overall, our analysis highlights the value of rangewide analyses of species' habitat relationships by bringing clarity to previous

work on smaller scales and enabling a “big picture” approach to defining the realized niche (Devictor et al., 2010; Soberón, 2007). Such large-scale efforts are especially important in an age where humans are not only shaping local landscapes through development but also transforming entire biomes and even the global ecosystem (Williams et al., 2015). These observations highlight the importance and utility of programs like Snapshot USA that collect standardized data across large geographic areas and allow broad-scale studies for evaluating the distribution and/or abundance of understudied species (Allen et al., 2022). If the Snapshot USA program (or other programs like it) were to continue for many years it would provide a wealth of ecological data for exploring the factors that affect species niches and distributions in order to inform conservation and management planning. As broad-scale datasets for wildlife species continue to become more common, local efforts can add much-needed nuance and context to rangewide patterns, thereby creating a richer understanding of species’ ecological and conservation that is firmly couched in a clear picture of species’ overall distribution and abundance.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The data is publicly available, as stated in the manuscript.

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